



The non-linear, interactive effects of population density and climate drive the geographical patterns of waterfowl survival

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ABSTRACT

On-going climate change has major impacts on ecological processes and patterns. Understanding the impacts of climate on the geographical patterns of survival can provide insights to how population dynamics respond to climate change and provide important information for the development of appropriate conservation strategies at regional scales. It is challenging to understand the impacts of climate on survival, however, due to the fact that the non-linear relationship between survival and climate can be modified by density-dependent processes. In this study we extended the Brownie model to partition hunting and non-hunting mortalities and linked non-hunting survival to covariates. We applied this model to four decades (1972–2014) of waterfowl band-recovery, breeding population survey, and precipitation and temperature data covering multiple ecological regions to examine the non-linear, interactive effects of population density and climate on waterfowl non-hunting survival at a regional scale. Our results showed that the non-linear effect of temperature on waterfowl non-hunting survival was modified by breeding population density. The concave relationship between non-hunting survival and temperature suggested that the effects of warming on waterfowl survival might be multifaceted. Furthermore, the relationship between non-hunting survival and temperature was stronger when population density was higher, suggesting that high-density populations may be less buffered against warming than low-density populations. Our study revealed distinct relationships between waterfowl non-hunting survival and climate across and within ecological regions, highlighting the importance of considering different conservation strategies according to region-specific population and climate conditions. Our findings and associated novel modelling approach have wide implications in conservation practice.

1. Introduction

On-going climate change has major impacts on ecological processes and patterns ranging from individual- to ecosystem-level (Grimm et al., 2013; Parmesan, 2006; Thomas et al., 2004; Walther, 2010), influencing population dynamics, extinction rates, and distributions of organisms (Keith et al., 2008; Moritz et al., 2008; Sæther et al., 2000; Sillett et al., 2000; Thomas et al., 2006). Models that explicitly examine the impacts of climate on the geographical patterns of demographic processes can provide insights to how populations respond to climate change across space and over time, and thus hold significance in ecological research and conservation practice (Gamelon et al., 2017; Sæther et al., 2004; Schippers et al., 2011). The impacts of climate on survival, one of the most important demographic parameters, have been examined in numerous taxa including plants (Reich and Oleksyn, 2008), insects (Paradis et al., 2008), fish (Ciannelli et al., 2007),

amphibians (Griffiths et al., 2010), reptiles (Tomillo et al., 2012), birds (Robinson et al., 2007), and mammals (Molnár et al., 2010), yet the non-linear, interactive effects of population density and climate factors on survival have rarely been examined.

A major challenge to understanding the effects of climate on survival lies in the fact that the relationship between survival and climate can be non-linear. A study in Scots pine (*Pinus sylvestris*) found that an increase in temperature had a positive effect on survival in the cold northern part of their study area, but had a negative effect on survival in the warm south (Reich and Oleksyn, 2008). Such a non-linear relationship represents complex effects of temperature on survival: while warmth may benefit survival in cold areas, high temperature may cause drought and thus reduce the chance of survival in warm areas. Studies in white stork (*Ciconia ciconia*) found that an increase in precipitation only had a positive effect on survival when precipitation was insufficient, but had no effect on survival when precipitation was

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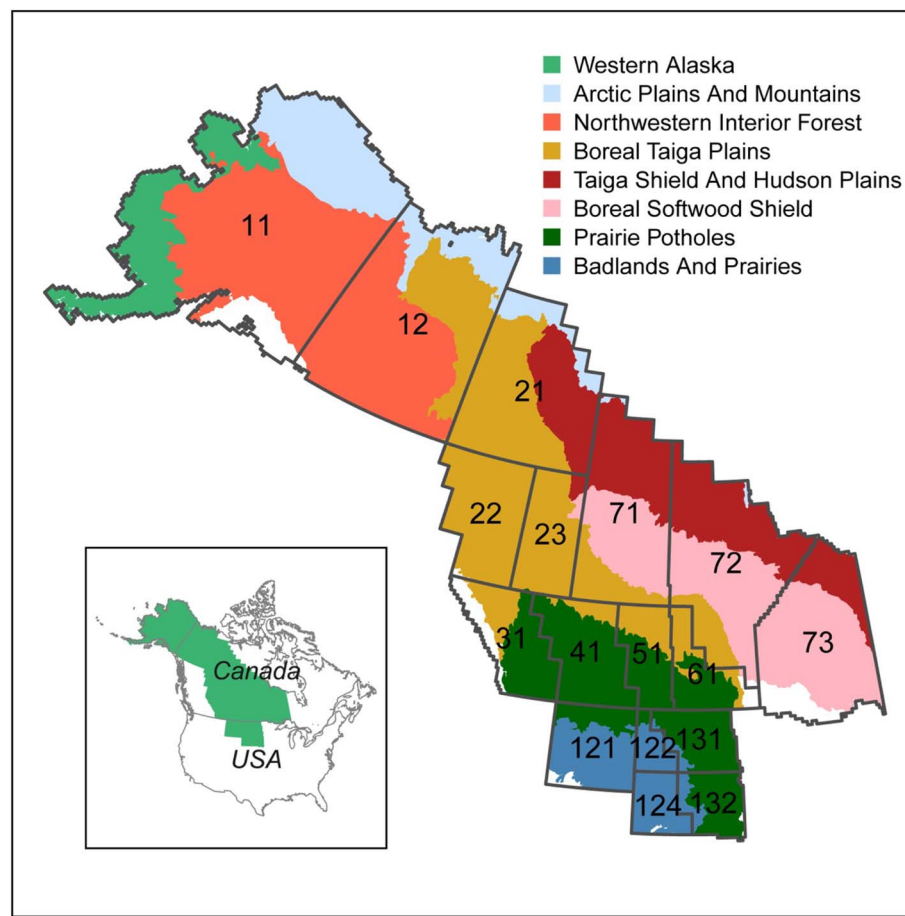


Fig. 1. The position of the study area in the North America (inner panel) and the relative position of reference areas (numbered) and ecological regions. Ecological regions are distinguished by colours shown in the legend. (For interpretation of the references to colour in this figure legend, the reader is referred to the online version of this chapter.)

abundant (Grosbois et al., 2008; Nevoux et al., 2008). While precipitation is normally considered beneficial to survival of water birds by increasing wetland habitat availability, it may also have a negative effect on their survival by reducing other important habitats, such as refugia, when high precipitation causes flood.

Alongside environmental stochasticity, density-dependent processes can also cause fluctuations in demography and population size, imposing another major challenge to understanding the effects of climate on survival. While the effects of density-dependent processes and environmental stochasticity are traditionally considered to be independent of each other, recent studies found that climate interacted with density-dependent processes to affect demography and population dynamics (Barbraud and Weimerskirch, 2003; Gamelon et al., 2017; Laws and Belovsky, 2010; Stenseth et al., 2004). Such interactions represent the fact that climate may influence resources that are essential for survival, and the competition over such resources is modified by population density (Gamelon et al., 2017). Incorporating the non-linear, interactive effects of population density and climate in model structures is important for studies that aim to identify and understand the regional and temporal variability in the relationship between survival and climate, providing information for the development of appropriate conservation strategies according to specific conditions at a regional scale.

The population size and demography of North American waterfowl populations have been monitored since the 1950's over a large spatial extent (Smith, 1995; U.S. Fish and Wildlife Service, 2012), providing a unique opportunity to understand the complex relationships among population density, climate, and survival at regional scales. The annual survival of these waterfowl populations is considered to be influenced

by wetland habitat availability (Nichols et al., 1982), which is in turn affected by climate change (Larson, 1995; Sofaer et al., 2016; Zhao et al., 2016). On the other hand, these waterfowl populations are also subjected to annual recreational harvest, which is affected by management decisions. Therefore, it is important to partition hunting and non-hunting mortality and examine the effects of population density and climate on non-hunting survival. Understanding the factors that drive waterfowl non-hunting survival is not only important for testing ecological hypotheses, but also key to the conservation management of waterfowl populations (Nichols et al., 2011). However, to our knowledge, no attempt has been made to examine the non-linear, interactive effects of population density and climate on the non-hunting survival of North American waterfowl populations, limiting our ability to manage these populations and their habitats under climate change.

In this study we aimed to understand the non-linear, interactive effects of density-dependent processes and climate on the spatio-temporal variation of waterfowl non-hunting survival. We extended the Brownie model (Brownie et al., 1985; Williams et al., 2002) to partition hunting and non-hunting mortality of waterfowl populations and linked non-hunting survival to covariates. We then applied the model to four decades (1972–2014) of Mallard (*Anas platyrhynchos*) band-recovery, breeding population survey, and climate data, which covers a large spatial extent from North American prairies through boreal habitats to Alaska. We examined the non-linear, interactive effects of breeding population density, temperature, and precipitation on Mallard non-hunting survival. We also identified distinct relationships between Mallard non-hunting survival and climate across and within ecological regions. We then sought to understand the implications of our results for the conservation of waterfowl as well as other wildlife populations

Table 1

Median and range (in brackets) of breeding population density, spring temperature, and winter precipitation for each reference area and the time period of the current study.

Area	Population density (N/100 km ²)	Temperature	Precipitation
11	180.2 [51.3, 354.9]	−11.1 [−17.3, −6.5]	82.0 [45.3, 116.3]
12	67.4 [23.9, 227.3]	−13.4 [−16.9, −8.6]	64.2 [40.3, 88.4]
21	71.5 [18.2, 161.9]	−12.2 [−16.9, −6.3]	47.7 [24.7, 137.2]
22	168.6 [58.9, 321.4]	−2.8 [−9.4, 0.9]	78.1 [51.4, 128.9]
23	213.3 [127.0, 472.2]	−3.0 [−10.3, 0.9]	67.0 [42.1, 103.7]
31	405.7 [269.4, 798.6]	−0.5 [−7.0, 2.3]	93.9 [61.7, 171.4]
41	601.5 [329.0, 1083.0]	0.4 [−7.2, 2.6]	68.7 [36.2, 112.2]
51	709.1 [340.3, 1198.1]	−1.4 [−7.8, 1.9]	75.8 [45.5, 131.4]
61	440.0 [198.5, 598.9]	−1.6 [−6.9, 3.0]	85.4 [48.9, 146.5]
131	412.5 [82.4, 1343.5]	1.2 [−5.4, 5.6]	73.3 [39.6, 148.8]
132	371.8 [100.1, 976.2]	4.3 [−1.1, 8.9]	111.7 [52.2, 201.4]
71	145.4 [46.3, 256.5]	−8.8 [−14.3, −2.9]	64.7 [30.8, 96.2]
72	156.2 [66.4, 291.3]	−8.9 [−12.6, −2.7]	71.8 [42.9, 122.0]
73	70.0 [28.5, 191.9]	−5.1 [−9.1, 0.7]	103.8 [52.2, 154.9]
121	154.4 [81.2, 315.8]	3.9 [−1.9, 7.0]	74.0 [34.6, 120.7]
122	282.1 [91.7, 611.4]	2.7 [−2.8, 6.8]	70.0 [28.2, 156.8]
124	183.8 [53.8, 524.5]	4.7 [0.6, 9.2]	96.9 [25.0, 167.5]

and their habitats under climate change.

2. Materials and methods

2.1. Study area and data collection

Our study area ranges from Montana, North Dakota, and South Dakota in the United States through the Canadian provinces of Alberta, Saskatchewan, Manitoba, and Ontario, including the Yukon and Northwest Territories, and Alaska (Fig. 1). The study area was delineated as 17 reference areas, which were defined by overlaying ecological regions and management areas. Ecological regions were defined based on a variety of ecological and biological factors including vegetation, hydrology, and terrain, and thus were used to represent different habitat conditions at a regional scale (Commission for Environmental Cooperation, 1997). For example, areas 31, 41, 51, 61, 131, and 132 overlap with the Prairie Pothole Region, which is considered to be the most important breeding habitat for North American waterfowls (Batt et al., 1989), and tends to have relatively high population density of Mallard populations in the study area (Table 1). Areas 21, 22, and 23, on the other hand, overlap with Boreal Taiga Plains that tends to have relatively low population density of Mallard populations (Table 1; Fig. 1). In addition to natural habitat conditions, anthropogenic activities that are different among management areas may further impose differences in population demography and population density within ecological regions (Bethke and Nudds, 1995). Therefore, we considered these reference areas as modelling units to examine distinct relationships between waterfowl non-hunting survival and covariates across and within ecological regions.

To estimate Mallard survival, wild Mallards were captured and

banded from July to September. Captured birds were banded with a standard leg band (USGS Bird Banding Laboratory), and for a subset of birds and years a band with at least \$100 reward was also applied. The cohorts (adult female and adult male) were determined upon banding. Recoveries included birds shot or found dead and reported to the U.S. Geological Survey Bird Banding Laboratory (BBL) or Canadian Bird Banding Office (BBO) during the hunting season (September to February) in any of the years after banding. The sample size of banding can be found in Appendix 1.

North American waterfowl breeding populations have been monitored annually since the 1950's by the U.S. Fish and Wildlife Service, Canadian Wildlife Service, and their partners during the Waterfowl Breeding Population and Habitat Survey (Smith, 1995; U.S. Fish and Wildlife Service, 2012). The survey covers the same areas as the banding effort. Aerial and ground surveys have been conducted simultaneously during May and June to identify and count Mallards as well as other waterfowl species. Mallard breeding population sizes were then estimated for each reference area while systematic observation errors in aerial survey were corrected using the information from ground survey (Pollock and Kendall, 1987; Smith, 1995). For details about the estimation of population size see Smith (1995).

We obtained temperature and precipitation data from climate data archives of the University of Delaware (Matsuura and Willmott, 2013a, 2013b). The temperature and precipitation data were interpolated from, and cross-validated with, weather station records by researchers from the University of Delaware (Matsuura and Willmott, 2013a, 2013b), and are available by month at a spatial resolution of $0.5 \times 0.5^\circ$ latitude/longitude. We calculated total winter (January to April) precipitation and mean spring (March to April) temperature for each reference area because these climate variables were shown to represent breeding season wetland habitat conditions (Zhao et al., 2016). The temporal correlation between local temperature and its mean for each reference area was high, and the temporal correlation between local precipitation and its mean for each reference area was moderately high (Appendix 2). We focused our analysis on the period of 1972 to 2014 due to data availability.

2.2. Model development

Traditionally, the relationship between annual survival and kill rate has been characterized as $S_t^{annual} = S^\varnothing \times (1 - \delta \times K_t)$, in which S_t^{annual} is annual survival in year t , $S^\varnothing$ is annual survival in the absence of hunting, K_t is kill rate, and δ is a parameter that governs the extent of compensation (small δ) or additivity (large δ) of anthropogenic mortality (Burnham and Anderson, 1984). This approach has been considered to be phenomenological because it defines a correlation between annual survival and hunting mortality without incorporating an underlying mechanism (Johnson et al., 1993). Further, because $S^\varnothing$ is normally unrealized in populations subjected to hunting, it is difficult to use this approach to examine the factors that drive non-hunting survival. It could also be risky to use this approach for the purpose of prediction if the underlying processes change over time.

Researchers have proposed an alternative approach to partition hunting and non-hunting mortalities such that $S_t^{annual} = (1 - K_t) \times S_t^{nh}$, in which S_t^{nh} was the probability that an individual survives non-hunting processes given that it survived hunting processes (Johnson et al., 1993). This approach provides an opportunity to characterize the relationship between non-hunting survival and covariates. However, to our knowledge this approach has not been used to understand waterfowl non-hunting survival in relation to population density and environmental conditions.

In this study we extended the Brownie et al. (1985) model to partition mortality due to hunting from non-hunting mortality. In the Brownie model, basic parameters include recovery rate (f_c , k , λ), the probability a banded individual alive at the beginning of the hunting season in year t is shot in that hunting season and reported to the BBL or

BBO, and annual survival rate ($S_{c,s,t}^{annual}$), the probability a banded individual survives an annual cycle between two banding periods. These parameters are indexed by c for cohort (adult female, adult male), k for band type (standard, reward), s for reference area, and t for year. We further let $f_{c,k,t} = K_{c,t} \times (1 - C) \times R_{k,t}$, in which $K_{c,t}$ is the probability an individual is killed during hunting season t , C (crippling loss rate) is the probability a hunter-killed bird is not retrieved by the hunter, and $R_{k,t}$ (band reporting rate) is the probability a retrieved bird with band type k is reported to either bird banding repository. We also let $S_{c,s,t}^{annual} = (1 - K_{c,t}) \times S_{c,s,t+1}^{nh}$, in which $S_{c,s,t+1}^{nh}$ is the probability that an individual survives non-hunting processes during an annual cycle given that it survived hunting processes.

We modelled kill rate with a random effect such that $\text{logit}(K_{c,t}) \sim \text{Normal}(\mu_c, \nu_c^2)$, with mean μ_c and variance ν_c^2 . In this way we allowed kill rate to change over time and used the random effect as an approach of borrowing information to facilitate the estimates of kill rate. The true, latent band reporting rate for standard bands ($R_{c=st,t}$) was estimated using a random walk model such that $\text{logit}(R_{c=st,t}) \sim \text{Normal}[\text{logit}(R_{c=st,t-1}), \psi_{RW}^2]$, in which ψ_{RW}^2 was the variance for the random walk. The random walk allowed gradual changes in band reporting rate over time. Further, we considered historical band reporting rate information ($R_{obs,t}$; Boomer et al. unpublished data) as realized observations of the true, latent band reporting rate such that $\text{logit}(R_{obs,t}) \sim \text{Normal}[\text{logit}(R_{c=st,t}), \psi_{obs}^2]$, in which ψ_{obs} was the standard error of $\text{logit}(R_{obs,t})$. We assumed reporting rate for birds recovered with reward bands was 1.0 (Nichols et al., 1991; Royle and Garrettson, 2005), and modelled the crippling loss rate with an informative prior such that $\text{logit}(C) \sim \text{Normal}[\text{logit}(0.2), 0.1]$ based on the results of previous studies (Anderson and Burnham, 1976; Martin and Carney, 1977).

We modelled non-hunting survival as a function of covariates such that

$$\begin{aligned} \text{logit}(S_{c,s,t}^{nh}) = & \alpha_c + \beta_{c,1} \times \ln BPOP_{s,t} + \\ & \beta_{c,2} \times TEMP_{s,t} + \beta_{c,3} \times TEMP_{s,t}^2 + \\ & \beta_{c,4} \times \ln BPOP_{s,t} \times TEMP_{s,t} + \beta_{c,5} \times \ln BPOP_{s,t} \times TEMP_{s,t}^2 + \\ & \beta_{c,6} \times PREC_{s,t} + \beta_{c,7} \times PREC_{s,t}^2 + \\ & \beta_{c,8} \times \ln BPOP_{s,t} \times PREC_{s,t} + \beta_{c,9} \times \ln BPOP_{s,t} \times PREC_{s,t}^2 + \\ & \varepsilon_{c,s,t} \end{aligned}$$

, in which $\ln BPOP_{s,t}$ was the log breeding population density for reference area s and year t , $TEMP_{s,t}$ was the spring temperature anomaly, and $PREC_{s,t}$ was the log winter precipitation. Breeding population density and precipitation were log transformed to stabilize their variance, whereas log transformation was not needed for temperature. Because log breeding population density, temperature, and log precipitation were standardized to have mean 0 and variance 1, α_c represented cohort-level mean non-hunting survival on the logit scale. We assumed residuals $\varepsilon_{c,s,t}$ followed iid normal distributions with mean 0 and variance σ_c^2 .

We conducted the analysis under a hierarchical Bayesian framework, using Markov Chain Monte Carlo methods via No-U-Turn sampling (NUTS) with the software Stan 2.6.2 (Lunn et al., 2000), which is called from R 3.0.2 (R Development Core Team., 2013) using R package “rstan” (Stan Development Team, 2014) to obtain the posterior distributions of the parameters. We used a vague prior distribution *Normal* (0, 100) for any mean, intercept, and slope terms, and a vague prior distribution *half-Cauchy* (0, 5) for any variance terms. We used five chains, each of which had 2500 iterations including 500 burn-in without thinning, resulting in 10,000 values for the posterior distribution of each parameter. Convergence of the MCMC computing was checked using trace-plots and “Rhat” statistics.

2.3. Understanding the relationships between non-hunting survival and covariates

We reported the posterior mean, standard deviation, and tail probability of parameter estimates. The tail probability was defined as the proportion of posterior samples that were smaller/larger than 0 when the posterior mean was positive/negative. We also used the posterior samples of parameter estimates to construct response curves between non-hunting survival and temperature/precipitation at high (97.5% quantile) or low (2.5% quantile) breeding population density to understand the non-linear, interactive effects of population density and climate on non-hunting survival. We borrowed the term “significance” from frequentist statistics and considered that the relationship between non-hunting survival and temperature/precipitation at high or low population density was significant if the 95% credible interval of the response curve could not contain a horizontal line, and insignificant otherwise. Finally, we plotted non-hunting survival against temperature for each reference area to understand the differences in the relationships between non-hunting survival and temperature across and within ecological regions.

3. Results

3.1. Effects of population density and climate on non-hunting survival

The posterior mean, standard deviation, and tail probability of parameter estimates were shown in Table 2. The estimated intercepts were equivalent to a 63.6% (95% C.I.: [61.8%, 65.3%]) mean non-hunting survival for adult females and a 79.8% (95% C.I.: [78.8%, 80.8%]) mean non-hunting survival for adult males at the population level. The response curves constructed based on the posterior samples showed that the relationship between non-hunting survival and temperature had a concave shape at high breeding population density for both adult females and adult males, and the relationship was non-significant at low population density (Fig. 2). The relationship between non-hunting survival and precipitation was non-significant at both high and low population densities for adult females and adult males (Fig. 2). Crippling loss rate had a posterior mean of 0.202 and 95% C.I. from 0.173 to 0.233.

3.2. Regional differences in survival-temperature relationship

Because the relationship between non-hunting survival and temperature was modified by population density, it showed distinct patterns across and within ecological regions. For example, the relationship between non-hunting survival and temperature showed a concave shape in all six areas (31, 41, 51, 61, 131, 132) overlapping with the

Table 2

The posterior mean, standard deviation, and tail probability of the intercept characterizing mean non-hunting survival and slopes characterizing the non-linear, interactive effects of log breeding population density ($\ln BPOP$), spring temperature ($TEMP$), and log winter precipitation ($PREC$) on non-hunting survival.

Covariate	Adult female			Adult male		
	Mean	S.D.	p-Tail	Mean	S.D.	p-Tail
Intercept	0.556	0.037	0.000	1.374	0.033	0.000
$\ln BPOP$	0.037	0.034	0.132	0.058	0.027	0.017
$TEMP$	0.001	0.032	0.490	-0.060	0.025	0.009
$TEMP^2$	-0.035	0.027	0.098	-0.078	0.019	0.000
$\ln BPOP \times TEMP$	-0.065	0.029	0.012	-0.071	0.023	0.001
$\ln BPOP \times TEMP^2$	-0.045	0.024	0.028	-0.049	0.019	0.005
$PREC$	0.019	0.032	0.276	-0.009	0.026	0.357
$PREC^2$	0.053	0.026	0.016	0.029	0.020	0.066
$\ln BPOP \times PREC$	-0.057	0.031	0.031	-0.011	0.025	0.331
$\ln BPOP \times PREC^2$	-0.015	0.020	0.222	-0.001	0.016	0.484

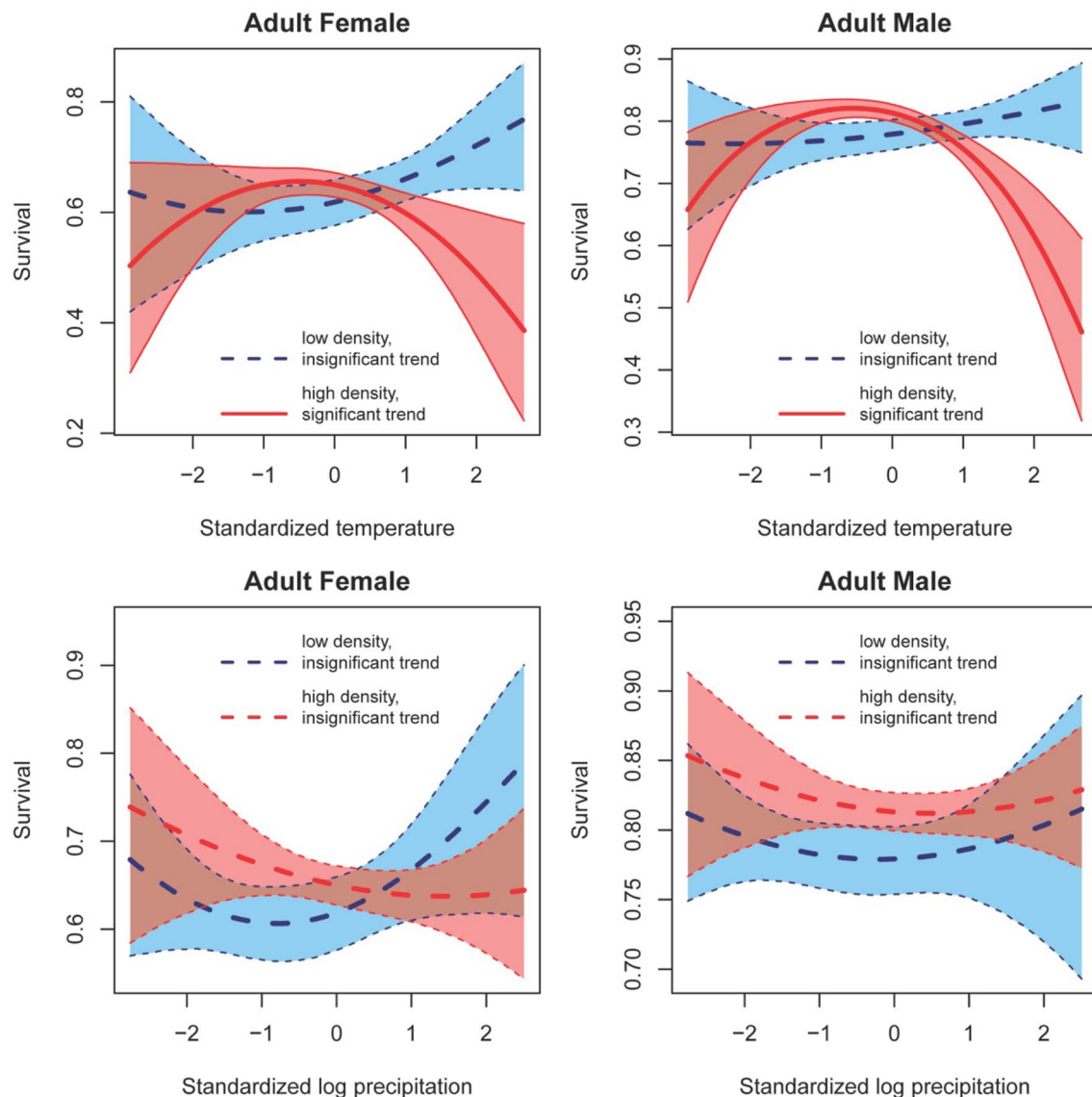


Fig. 2. The response curve between non-hunting survival and standardized temperature (higher panels) or standardized log precipitation (lower panels) at high (95% quantile; red) or low (5% quantile; blue) breeding population density for adult females (left panels) and adult males (right panels). The fitted line is solid if the relationship is significant (i.e. 95% credible interval cannot contain a horizontal line), and broken otherwise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Prairie Pothole Region. By contrast, the concave relationship between non-hunting survival and temperature was only found in the two southern areas (22, 23) overlapping with the Boreal Taiga Plains, but not in the northern area (21) overlapping with the same ecological region (Fig. 3).

4. Discussion

By partitioning hunting and non-hunting mortality and linking non-hunting survival to population density and climate covariates, we found that the non-linear effect of temperature on Mallard non-hunting survival was modified by breeding population density. Consequently, the relationship between non-hunting survival and temperature showed distinct patterns across and within ecological regions, due to the differences in population density. Our findings associated with the modelling approach have important implications for the conservation of waterfowl as well as other wildlife populations and their habitats in response to climate change.

4.1. The effects of population density and temperature on non-hunting survival

In this study we found that the relationship between Mallard non-hunting survival and temperature had a concave shape at high breeding population density. The negative effect of temperature under warm conditions suggests that the increase in temperature may reduce waterfowl survival by causing drought. However, we also found that the increase in temperature could benefit waterfowl survival under cold conditions. This may be due to the fact that warmth can facilitate the growth of aquatic plants (Carr et al., 1997), which are often consumed by waterfowl species as food. Thus the effects of temperature on waterfowl survival may be multifaceted. The positive effect of temperature on survival seems to overcome its negative effect under cold conditions, but the opposite seems to be true under warm conditions.

Furthermore, the non-hunting survival of Mallards seems to be sensitive to temperature when population density is high, but not influenced by temperature when population density is low. This may reflect the fact that the changes in temperature lead to changes in

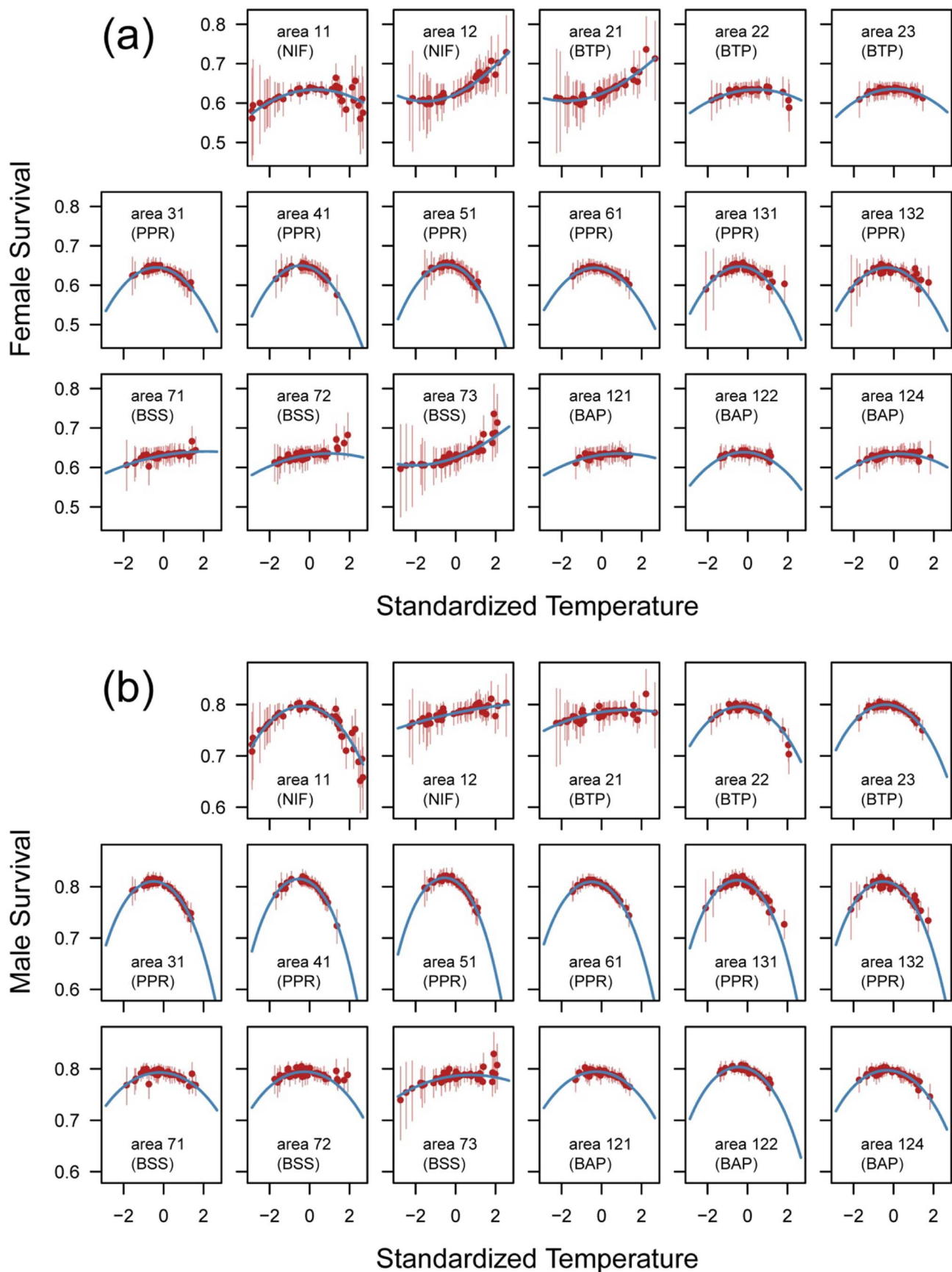


Fig. 3. The relationship between non-hunting survival of (a) adult females and (b) adult males and standardized temperature for each reference area. Red points and lines represent non-hunting survival and associated 95% Credible Intervals for each year, and blue lines represent predicted relationship under the mean population density of the corresponding area. Each plot corresponds to a reference area. The abbreviation of the ecological region each reference area mainly overlaps with is shown in parentheses: NIF: Northwestern Interior Forest, BTP: Boreal Taiga Plains, PPR: Prairie Potholes, BSS: Boreal Softwood Shield, BAP: Bandlands and Prairies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resources (e.g. wetland habitat and food) that are important to waterfowl survival, but the changes in resources may only influence survival when competition is strong at high population density, and become less influential to survival when competition is weak at low population density. The interactive effect of population density and environmental condition on population demography and dynamics has been found in other taxa (Barbraud and Weimerskirch, 2003; Gamelon et al., 2017; Laws and Belovsky, 2010; Stenseth et al., 2004). For example, Barbraud and Weimerskirch (2003) found that a combination of poor oceanographic conditions and high population density lead to low winter survival of blue petrels; Gamelon et al. (2017) found that climate conditions mainly affect the demography of white-throated dipper populations at high population densities; and Laws and Belovsky (2010) found that warm condition has a negative effect on grasshopper survival at high density, but not at low density. Overall, our results are consistent with the prediction that the effects of environmental conditions on demography are modified by density dependent processes, and highlight the importance of considering the non-linear, interactive effects of population density and environmental conditions to understand the spatial and temporal variation of demography.

Because the relationship between waterfowl non-hunting survival and temperature is modified by population density, we found distinct relationships between non-hunting survival and temperature across and within ecological regions. For example, the relationship between non-hunting survival and temperature showed a concave shape in all six areas overlapping with the Prairie Pothole Region, due to the fact that population density is high in this ecological region. The Boreal Taiga Plain, on the other hand, shows a strong spatial gradient in population density such that population density in the southern part is two to three times higher than that in the northern part of this ecological region (Table 1). Consequently, the relationship between non-hunting survival and temperature is also different between south and north in this ecological region.

Spatial variability in population-environment relationships has been found in many taxa such as plants, birds, and mammals (Forchhammer et al., 1998; Grøtan et al., 2009; Reich and Oleksyn, 2008; Williams et al., 2003). While such a phenomenon may reflect the fact that relationships between natural populations and environmental conditions can be modified by population densities, the underlying demographic foundation of such a phenomenon has rarely been examined. For example, the relationships between waterfowl population growth and environmental conditions have been described to vary along latitude (Sæther et al., 2008), between core and peripheral habitat (Feldman et al., 2015), or among ecological regions (Zhao et al., 2016), yet the interactive effects of population density and environmental conditions on the underlying demographic processes have not been examined. In a previous study Zhao et al. (2016) found that pond numbers had a stronger effect on Mallard population size in Prairie Pothole Region than in Boreal Taiga Plains, which may be due to the difference in population density between these two ecological regions. The non-linear, interactive effects of population density and temperature on waterfowl survival revealed in this study could provide important insights for the spatial variability in the relationships between environmental conditions and waterfowl populations. Because the spatial variability in population-environment relationships is commonly found in many taxa, we believe that the importance of considering the non-linear, interactive effects of population density and environmental conditions on population demography is not limited to waterfowl.

4.2. Future directions

While our study revealed important non-linear, interactive effects of population density and temperature on waterfowl non-hunting survival, we believe that the study can be further improved in at least two

directions. First, while local temperature is highly correlated to its mean at the spatial scale of reference areas, local precipitation shows relatively high heterogeneity within each reference area, and thus is only moderately correlated to its area mean (Appendix 2). This may explain why we failed to detect significant relationship between waterfowl non-hunting survival and precipitation. Further studies are needed to examine the relationship between non-hunting survival and precipitation at relatively fine spatial scales. Second, we decided not to address movement among areas in this study because adult Mallards have been shown to have high site fidelity (Doherty et al., 2002) and the spatial scale we examined is relatively large. We acknowledge that further studies could consider incorporating movement in model structure (Schwarz et al., 1993), particularly when conducting analyses at fine spatial scales.

4.3. Implications for wildlife conservation

Our findings associated with the modelling approach hold significance in the conservation of waterfowl, and in general wildlife populations and their habitats. While warming is traditionally considered to be harmful to wildlife populations by causing drought, our results suggest that the effects of warming may be multifaceted. Further, the interactive effect of population density and climate on survival suggests that high-density populations may be less buffered against warming than low-density populations. The distinct relationships between survival and temperature across space imply that wildlife populations may respond to climate change differently at regional scales, and population and habitat managers may want to choose different, but appropriate conservation strategies according to the specific population and climate conditions in each region. For example, while waterfowl survival in the Prairie Pothole Region is likely to decrease under future warming, waterfowl populations in the northern Boreal Taiga Plains seem to be relatively buffered against warming. Consequently, strategies that reduce the risk of population decrease may be appropriate for the Prairie Pothole Region, whereas the Northern Boreal Taiga Plains may serve as refugia for waterfowl populations under climate change. Furthermore, because the relationship between survival and climate is modified by population density, such relationship may change in the future when population density varies under climate change. Therefore, long-term population monitoring is essential for the development of conservation strategies that can promptly adapt to the changes in both population status and climate. Because the non-linear, interactive effects of population density and climate on survival and population dynamics have been found in other species and ecosystems (Gamelon et al., 2017; Laws and Belovsky, 2010; Reich and Oleksyn, 2008), the importance of long-term population monitoring is not limited to any specific taxon and habitat. Therefore, we believe that our findings can have wide implications in conservation practices.

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Appendix 1. The number of banding stations, the total number of bands during the study period, and the number of years (out of 43) with banding for each reference area.

Area	Number of banding stations	Total number of bands	Number of years with banding
11	1402	9499	33
12	747	10,965	35
21	2310	32,224	42
22	845	75,348	35
23	690	4011	10
31	1000	192,695	43
41	1080	265,016	43
51	654	133,422	42
61	642	189,350	43
71	1722	14,078	25
72	2139	2073	15
73	2235	7922	31
121	864	27,077	41
122	216	3427	21
124	360	3705	16
131	548	110,923	43
132	459	52,985	36

Appendix 2. The temporal correlation between local climate condition and its mean for each reference area. Median and 95% credible interval (in brackets) are shown.

Area	Temperature	Precipitation
11	0.83 [0.62, 0.96]	0.52 [0.07, 0.72]
12	0.84 [0.70, 0.97]	0.47 [0.23, 0.74]
21	0.83 [0.66, 0.95]	0.55 [0.20, 0.90]
22	0.95 [0.80, 0.98]	0.74 [0.37, 0.92]
23	0.97 [0.92, 0.99]	0.69 [0.51, 0.85]
31	0.94 [0.63, 0.98]	0.70 [0.46, 0.86]
41	0.97 [0.90, 0.99]	0.70 [0.48, 0.84]
51	0.98 [0.95, 0.99]	0.74 [0.51, 0.92]
61	0.98 [0.93, 0.99]	0.81 [0.40, 0.92]
71	0.97 [0.87, 0.99]	0.72 [0.16, 0.89]
72	0.95 [0.81, 0.99]	0.73 [0.20, 0.83]
73	0.91 [0.80, 0.97]	0.69 [0.45, 0.85]
121	0.97 [0.86, 0.99]	0.76 [0.52, 0.89]
122	0.99 [0.97, 0.99]	0.84 [0.72, 0.94]
124	0.97 [0.92, 0.99]	0.81 [0.63, 0.93]
131	0.98 [0.94, 0.99]	0.79 [0.59, 0.90]
132	0.98 [0.95, 0.99]	0.80 [0.56, 0.92]

References

- Anderson, D.R., Burnham, K.P., 1976. Population Ecology of the Mallard: VI. The effect of Exploitation on Survival. US Fish and Wildlife Service.
- Barbraud, C., Weimerskirch, H., 2003. Climate and density shape population dynamics of a marine top predator. *Proc. R. Soc. Lond. B Biol. Sci.* 270, 2111–2116.
- Batt, B.D., Anderson, M.G., Anderson, C.D., Caswell, F.D., 1989. The use of prairie potholes by North American ducks. In: van der Valk, A. (Ed.), *Northern Prairie Wetlands*. Iowa State University, Ames, USA, pp. 204–227.
- Bethke, R.W., Nudds, T.D., 1995. Effects of climate change and land use on duck abundance in Canadian prairie-parklands. *Ecol. Appl.* 5, 588–600.
- Brownie, C., Anderson, D.R., Burnham, K.P., Robson, D.S., 1985. Statistical Inference From Band Recovery Data: A Handbook.
- Burnham, K.P., Anderson, D.R., 1984. Tests of compensatory vs. additive hypotheses of mortality in mallards. *Ecology* 65, 105–112.
- Carr, G.M., Duthie, H.C., Taylor, W.D., 1997. Models of aquatic plant productivity: a review of the factors that influence growth. *Aquat. Bot.* 59, 195–215.
- Ciannelli, L., Dingsør, G.E., Bogstad, B., Ottersen, G., Chan, K.-S., Gjøsæter, H., Stiansen, J.E., Stenseth, N.C., 2007. Spatial anatomy of species survival: effects of predation and climate-driven environmental variability. *Ecology* 88, 635–646.
- Commission for Environmental Cooperation, 1997. Ecological Regions of North America: Toward a Common Perspective. Commission for Environmental Cooperation.
- Doherty, P.F., Nichols, J.D., Tautin, J., Voelzer, J.F., Smith, G.W., Benning, D.S., Bentley, V.R., Bidwell, J.K., Bollinger, K.S., Brazda, A.R., 2002. Sources of variation in breeding-ground fidelity of mallards (*Anas platyrhynchos*). *Behav. Ecol.* 13, 543–550.
- Feldman, R.E., Anderson, M.G., Howerter, D.W., Murray, D.L., 2015. Where does environmental stochasticity most influence population dynamics? An assessment along a regional core-periphery gradient for prairie breeding ducks. *Glob. Ecol. Biogeogr.* 24, 896–904.
- Forchhammer, M.C., Stenseth, N.C., Post, E., Landvatn, R., 1998. Population dynamics of Norwegian red deer: density–dependence and climatic variation. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 265, 341–350.
- Gamelon, M., Grøtan, V., Nilsson, A.L., Engen, S., Hurrell, J.W., Jerstad, K., Phillips, A.S., Røstad, O.W., Slagsvold, T., Walseng, B., 2017. Interactions between demography and environmental effects are important determinants of population dynamics. *Sci. Adv.* 3, e1602298.
- Griffiths, R.A., Sewell, D., McCrea, R.S., 2010. Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. *Biol. Conserv.* 143, 485–491.
- Grimm, N.B., Chapin, F.S., Bierwagen, B., Gonzalez, P., Groffman, P.M., Luo, Y., Melton, F., Nadelhoffer, K., Pairis, A., Raymond, P.A., 2013. The impacts of climate change on ecosystem structure and function. *Front. Ecol. Environ.* 11, 474–482.
- Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Møller, A., Weimerskirch, H., 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* 83, 357–399.
- Grøtan, V., Sæther, B.E., Engen, S., Van Balen, J.H., Perdeck, A.C., Visser, M.E., 2009. Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations. *J. Anim. Ecol.* 78, 447–459.
- Johnson, F.A., Williams, B., Nichols, J., Hines, J.E., Kendall, W., Smith, G., Caithamer, D., 1993. Developing an adaptive management strategy for harvesting waterfowl in North America. In: *Transactions of the North American Wildlife and Natural Resources Conference (USA)*.
- Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B., Rebelo, T.G., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* 4, 560–563.
- Larson, D.L., 1995. Effects of climate on numbers of northern prairie wetlands. *Clim. Change* 30, 169–180.
- Laws, A.N., Belovsky, G.E., 2010. How will species respond to climate change? Examining the effects of temperature and population density on an herbivorous insect. *Environ. Entomol.* 39, 312–319.
- Lunn, D.J., Thomas, A., Best, N., Spiegelhalter, D., 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. *Stat. Comput.* 10, 325–337.
- Martin, E.M., Carney, S.M., 1977. Population Ecology of the Mallard IV: A Review of Duck Hunting Regulations, Activity, and Success, with Special Reference to the Mallard. US Fish and Wildlife Service.
- Matsuura, K., Willmott, C.J., 2013a. Terrestrial Air Temperature: 1900–2010 Gridded Monthly Time Series (V. 3.02).
- Matsuura, K., Willmott, C.J., 2013b. Terrestrial Precipitation: 1900–2010 Gridded Monthly Time Series (V. 3.02).
- Molnár, P.K., Derocher, A.E., Thiemann, G.W., Lewis, M.A., 2010. Predicting survival, reproduction and abundance of polar bears under climate change. *Biol. Conserv.* 143, 1612–1622.
- Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C., Beissinger, S.R., 2008. Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* 322, 261–264.
- Nevoux, M., Barbraud, J.C., Barbraud, C., 2008. Nonlinear impact of climate on survival in a migratory white stork population. *J. Anim. Ecol.* 77, 1143–1152.
- Nichols, J.D., Pospahala, R.S., Hines, J.E., 1982. Breeding-ground habitat conditions and the survival of Mallards. *J. Wildl. Manag.* 46, 80–87.
- Nichols, J.D., Blohm, R.J., Reynolds, R.E., Trost, R.E., Hines, J.E., Bladen, J.P., 1991. Band reporting rates for mallards with reward bands of different dollar values. *J. Wildl. Manag.* 55, 119–126.
- Nichols, J.D., Koneff, M.D., Heglund, P.J., Knutson, M.G., Seamans, M.E., Lyons, J.E., Morton, J.M., Jones, M.T., Boomer, G.S., Williams, B.K., 2011. Climate change, uncertainty, and natural resource management. *J. Wildl. Manag.* 75, 6–18.
- Paradis, A., Elkinton, J., Hayhoe, K., Buonaccorsi, J., 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitig. Adapt. Strateg. Glob. Chang.* 13, 541–554.
- Parnesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Pollock, K.H., Kendall, W.L., 1987. Visibility bias in aerial surveys: a review of estimation procedures. *J. Wildl. Manag.* 51, 502–510.
- R Development Core Team, 2013. R: A Language and Environment for Statistical Computing.
- Reich, P., Oleksyn, J., 2008. Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecol. Lett.* 11, 588–597.
- Robinson, R.A., Baillie, S.R., Crick, H.Q., 2007. Weather-dependent survival: implications of climate change for passerine population processes. *Ibis* 149, 357–364.
- Royle, J.A., Garrettson, P.R., 2005. Research notes: the effect of reward band value on mid-continent mallard band reporting rates. *J. Wildl. Manag.* 69, 800–804.
- Sæther, B.-E., Tufto, J., Engen, S., Jerstad, K., Røstad, O.W., Skåtan, J., 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287, 854–856.
- Sæther, B.-E., Sutherland, W.J., Engen, S., 2004. Climate influences on avian population dynamics. *Adv. Ecol. Res.* 35, 185–209.
- Sæther, B.E., Lillegård, M., Grøtan, V., Drever, M.C., Engen, S., Nudds, T.D., Podrutzny, K.M., 2008. Geographical gradients in the population dynamics of North American prairie ducks. *J. Anim. Ecol.* 77, 869–882.
- Schippers, P., Verboom, J., Vos, C.C., Jochem, R., 2011. Metapopulation shift and survival of woodland birds under climate change: will species be able to track? *Ecography* 34, 909–919.
- Schwarz, C.J., Schweigert, J.F., Arnason, A.N., 1993. Estimating migration rates using tag-recovery data. *Biometrics* 177–193.
- Sillett, T.S., Holmes, R.T., Sherry, T.W., 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288, 2040–2042.
- Smith, G.W., 1995. A Critical Review of the Aerial and Ground Surveys of Breeding Waterfowl in North America. DTIC Document.
- Sofaer, H.R., Skagen, S.K., Barsugli, J.J., Rashford, B.S., Reese, G.C., Hoeting, J.A., Wood, A.W., Noon, B.R., 2016. Projected wetland densities under climate change: habitat loss but little geographic shift in conservation strategy. *Ecol. Appl.* 26, 1677–1692.
- Stan Development Team, 2014. Stan: a C++ Library for Probability and Sampling.
- Stenseth, N.C., Chan, K.-S., Tavecchia, G., Coulson, T., Mysterud, A., Clutton-Brock, T., Grenfell, B., 2004. Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proc. R. Soc. Lond. B Biol. Sci.* 271, 1985–1993.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thomas, C.D., Franco, A.M., Hill, J.K., 2006. Range retractions and extinction in the face of climate warming. *Trends Ecol. Evol.* 21, 415–416.
- Tomillo, P.S., Saba, V.S., Blanco, G.S., Stock, C.A., Paladino, F.V., Spotila, J.R., 2012. Climate driven egg and hatchling mortality threatens survival of Eastern Pacific leatherback turtles. *PLoS One* 7, e37602.
- U.S. Fish and Wildlife Service, 2012. Waterfowl Population Status, 2012.
- Walther, G.-R., 2010. Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 365, 2019–2024.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. Analysis and Management of Animal Populations. Academic Press.
- Williams, C.K., Ives, A.R., Applegate, R.D., 2003. Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology* 84, 2654–2667.
- Zhao, Q., Silverman, E., Fleming, K., Boomer, G.S., 2016. Forecasting waterfowl population dynamics under climate change—does the spatial variation of density dependence and environmental effects matter? *Biol. Conserv.* 194, 80–88.